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DIMINUTIVE EPIBIONTS ON CRINOID STEMS FROM THE LOWER/MIDDLE DEVONIAN BOUNDARY IN THE BARRANDIAN, CZECH REPUBLIC

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Abstract: *Diminutive crinoid holdfasts and cemented tests of the foraminifers Psammosphaera and Tolypammina were observed on coarse bioclasts in weathered limestones of the Daleje-Třebotov Formation. Specimens were obtained in 1984 by washing so called "white beds" at a temporary locality in Praha-Barrandov. A few millimeter sized bioclasts with epibionts were freed from hard limestone beds of the Třebotov Limestone near the Lower/Middle Devonian boundary by long-term weathering. Many of the crinoid holdfasts attached to pluricolumnals provoked a stereomic response of the host crinoid. Also the growth orientation of the crinoid epibiont is not random and indicates some crinoid-epibiont to crinoid-host interaction. Reaction of host stereome and non-random stem orientation offer direct evidence of epibiont larval settlement and subsequent growth on the stem of a living crinoid host. The extensive growth of the host stereome ended by partial to total engulfing of the epibiont holdfast. This indicates advancing and finally successful defence of the host crinoid against the epibiont. The holdfast gives evidence that the small host crinoids offered a somewhat higher tier for even smaller epibiont crinoids. However, other observed holdfasts indicate fixation of larva and growth over loose bioclasts lying on a sea bed. Location of foraminifer test on bioclasts confims that foraminifers cemented and grew on loose echinodermal and brachiopod remains and preferred crevices and similar protected sites with concave profiles. This is clear evidence that diverse bioclasts (brachiopod shells, pelmatozoan ossicles) provided the hard substrate suitable for epibiont life on a sea bed.*

Key words: Crinoids, holdfasts, microcrinoids, epibionts, Devonian, Eifelian, Třebotov Formation, Prague Basin.

INTRODUCTION

Crinoidal limestone, dominantly assembled from stems and columnals, is the most characteristic carbonate sediment of Silurian and Devonian times. The Barrandian area of the Central Bohemia is not an exception. Columnals and pluricolumnals are the dominant component of the perireefal Kotýs, Slivenec, Řeporyje, Vinařice, Loděnice and Třebotov limestones spanning Lochkovian to Eifelian ages. In many sites in close vicinity of Praha the limestone rocks were subjected by deep and long-term weathering processes. Their micritic component disintegrated into soft residue (so called "white beds") while the calcitic skeletal debris (pelmatozoan ossicles, brachiopods, gastropods, bivalves, hyolithids, dacryoconarids and other shells, annelid plates etc.) have been released from hard rock (Petr *et al.* 1997). These loose and often unique fossils generally display excellent details. Therefore, they were intensively collected and were studied since the beginning of the 20th century.

Unlike brachiopods (Havlíček 1956, 1998, Havlíček & Vaněk 1998), gastropods (Horný 1955, 1963, 1964, Frýda 1998, 1999a, 1999b, Frýda & Bandel 1997), annelids (Prokop 2002), eleutherozoans (Prokop 1993, Prokop & Petr 1986, Hotchkiss *et al.* 1999a, 1999b, 2007), pelmatozoan columnals (Slámová & Prokop 2000, Prokop & Slámová 2008, 2012, Prokop 2009, 2013, Prokop & Nohejlová 2015), crinoid crowns and calyxes

(Prokop 1969, 1970, 1976, 1977, 1980, 1982a, 1982b, 1986, 1997, Prokop & Petr 1987, 1988, 1991, 1993, 1998, 2010) or other pelmatozoan ossicles (Prokop & Petr 2002, 2004), the crinoid holdfasts were only briefly mentioned among washed fossils of white beds (Petr 1983, Galle & Prokop 2000). Like the other shells, crinoid holdfasts and small epibiots attached to crinoid columnals and stems are excellently preserved. They provide reliable insight into life strategies and autecology of epibionts on a sea bed covered by loose pelmatozoan debris.

GEOLOGICAL SETTING

The locality carrying described epibionts lies at the northeast limb of the Devonian infilling of the Prague Basin in the Central Bohemia of Czechia (Czech Republic; Figure 1A, B). The Devonian succession of the Prague Basin starts with carbonate deposits of the Lochkov Formation (Lochkovian) and continues to the siliciclastic Srbsko Formation (Givetian). The Lochkovian to Eifelian succession is characterised by shallow water, perireefal mostly crinoidal limestones, and in a smaller extension, also reef bioskeletal accumulations of Pragian to Eifelian age. Dark coloured calcisiltites situated more south-eastwardly represent the pelagic lithofacies of the same age. The overlying siliciclastic Givetian succession indicates the beginning of the Variscan orogeny (Chlupáč 1998, Vacek & Žák 2019).

The Třebotov Limestone is a perireefal member of the Daleje-Třebotov Formation (Upper Emsian). In the parastratotype Prastav Quarry its upper limestone beds are of early Eifelian age (Chlupáč 1982, 1985, Klapper *et al.* 1978). The base of the succeeding Choteč Limestone (Eifelian) is marked by the manifestation of the Choteč Event. Dark shale intercalations, the darker tones of limestone, and an increase of micrite content strikingly distinguishes the Choteč Limestone from the preceding Třebotov Limestone.

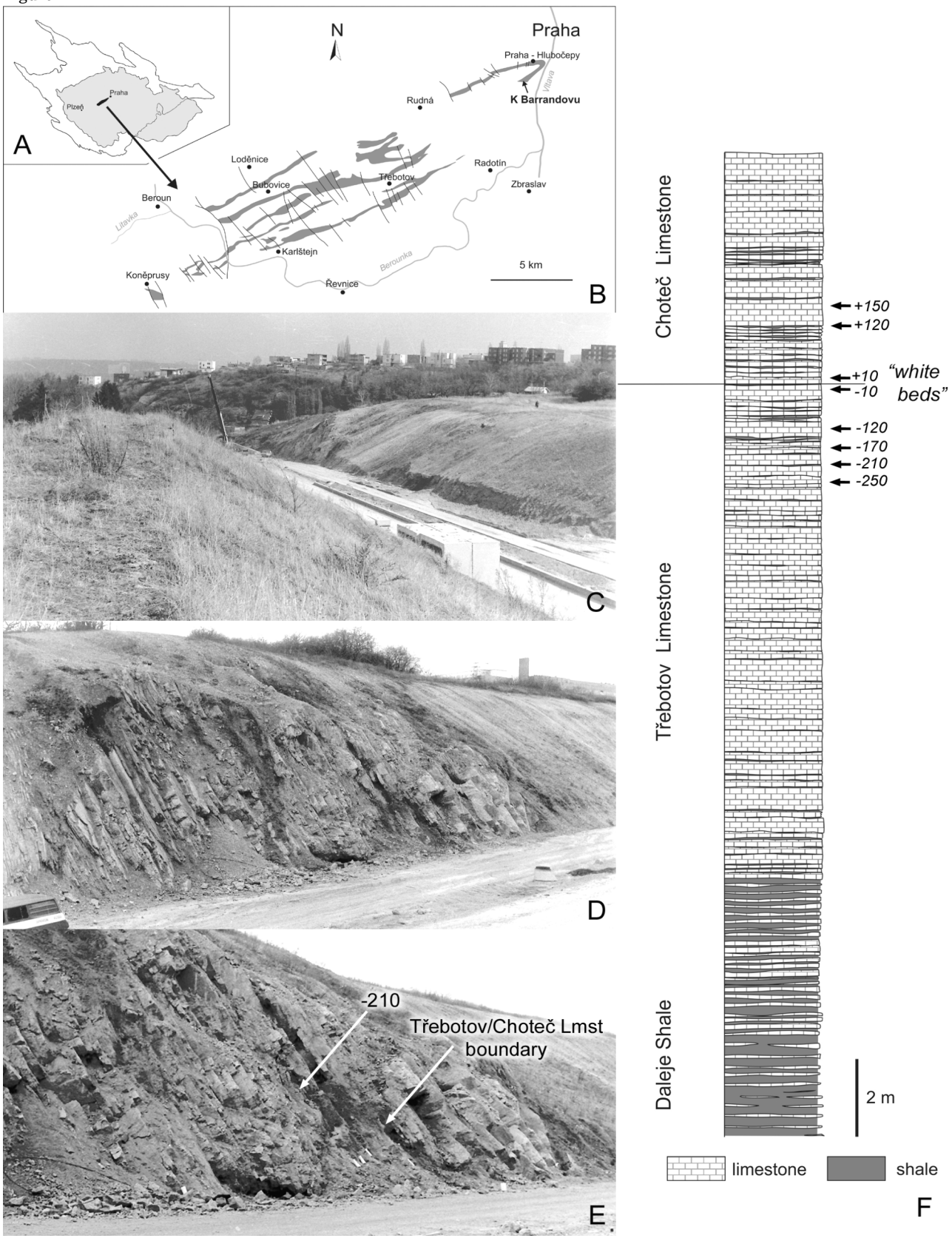
Fossil distribution near Lower/Middle Devonian boundary, and Třebotov/Choteč limestones boundary, respectively, are satisfactory documented in the international parastratotype Prastav Quarry at Praha-Holyně (Chlupáč 1982, 1998). The equivalent succession of the Třebotov and Choteč limestones, only 2600 m east from the parastratotype, was temporarily accessible in the excavation of the roadcut at Praha-Barrandov in 1984 (Figure 1C–E). Unlike the Prastav Quarry section, the limestone beds in the uppermost Třebotov Limestone and the lowermost Choteč Limestone in the road cut were deeply weathered into yellowish soft material ("white beds"). These beds provided exceptionally rich and well preserved fossils. The assemblage contains dacryoconarids, conodonts, ostracods, echinoderms, brachiopods, gastropods, hyoliths, goniatites, trilobites, annelids and bivalves. Only dacryoconarids (Lukeš 1989), ostracods (Šlechta 1996), conodonts (Zusková 1991, Berkyová 2009, Berkyová *et al.* 2009) and selected groups of echinoderms (Prokop & Petr 1991, Prokop 1997, Prokop & Nohejlová 2015) were described to date. The Barrandov section covers the *P. serotinus* to *P. australis* zones (Berkyová 2009). The studied material of "white beds" came from the upper part of the *P. costatus partitus* Zone (Berkyová 2009).

MATERIAL AND METHODS

The described epibionts come from the "white beds" sampled 200 to 220 cm below the base of the Choteč Limestone (sample Barr: –210; Figure 1E, F). In total, more than 10 thousand echinoderm ossicles were picked out under a binocular microscope from a size fraction larger than 2 mm. Smaller bioclasts were eliminated from a epibiont calculation. 5620 crinoid columnals, 106 pluricolumnals (= two and more columnals jointed together) and 615 other crinoid ossicles were examined for the presence of epibionts. Ultrasonic cleaning was not used due to the brittleness of fossils. Therefore, ossicles with epibionts were

Figure 1. *Geographical setting of the Devonian in the Bohemian Massif and the Czech Republic (A); the Daleje-Třebotov and Choteč formations (Upper Emsian to Eifelian) in the Prague Basin (B); the road cut in Praha-Barrandov (C); the road cut section with the Třebotov Limestone (left to centre), Choteč Limestone (right) followed with siltstone beds of the Srbsko Formation (Givetian) in the background (D); the road cut section with marked location of sample Barr: –210 and Třebotov/Choteč limestones boundary (E); the road cut section with marked "white beds" samples. All photos came from field work conducted in 1984.*

Figure 1


A
Praha
Plzeň
N
Praha
Praha - Hlubočepy
K Barrandovu
Rudná
Vltava
Loděnice
Radotín
Třebotov
Zbraslav
Beroun
Litavka
Karlštejn
Berounka
Koněprusy
Řevnice
5 km
B
C
D
-210
Třebotov/Choteč Lmst
boundary
E
Choteč Limestone
Třebotov Limestone
Daleje Shale
+150
+120
+10
-10
"white beds"
-120
-170
-210
-250
2 m
limestone
shale
F

cleaned only by fine brushes. Cleaned specimens were lightly whitened by ammonium chloride before taking photos by a Canon camera mounted on an Olympus SZX7 binocular microscope. The pictures were processed by Deep Focus QuickPhoto Micro 3.2. software. The position of the epizoan crinoid was assessed relative to the orientation of a host crinoid stem. Measurements were made parallel to the direction of the epizoan stalk relative to the elongation of the host stalk (Figure 2A), and the divergence angle of epizoan stalk from a host stalk surface was also measured (Figure 2B).

Terminology generally follows that of Moore & Teichert (1978) and Franzén (1977). All specimens are stored in the palaeontological collections of the West Bohemia University at Plzeň (PCZCU 2487 to PCZCU 2540).

EPIBIONT HOLDFASTS

The mode of life in Palaeozoic crinoids is quite well known. Most of them were sedentary, permanently fixed to sea floor by attachment discs, cirriferous holdfasts, creeping stems or other modifications of the distal part of the stem (Franzén 1977). Other crinoids were vagile with the stem capable of coiling around supporting objects (Franzén 1977) or floating by means of a unique gas filled device (Shrock & Twenhofel 1953). Some holdfasts were robust and extensive with numerous pseudocirri (Franzén 1977) or a large complex root system (Halleck 1973), but others were diminutive having sparsely stellate outline and smooth surface, representing remains of juvenile crinoids or bases of microcrinoids (Głuchowski 2005). According to Franzén (1977), a thin calcified membrane or a cuticular layer on the lower side of the discoid holdfast served as an adhesive surface. Holdfasts grew by concentric layers of stereome expanding both vertically and horizontally. A fine net of radiating canals inside a holdfast distributed nutrients (Franzén 1977).

Our material of crinoid attachment devices comprises (1) rhizoid holdfasts attached to stalks, isolated columnals or other cylindrical objects, (2) stellate and lobate holdfasts attached to planar and irregular subplanar surfaces, and (3) cirral holdfasts. All holdfasts are diminutive and not exceeding 5 millimeters in size.

Rhizoid holdfasts

Plate I; Plate III, figs 1–3

Material: 25 holdfasts attached to crinoid columnals or pluricolumnals, and two loose holdfasts: figured specimens (PCZCU 2487, PCZCU 2491–2495, PCZCU 2497, PCZCU 2514–2519, PCZCU 2522, PCZCU 2526, PCZCU 2532) and six unfigured specimens.

Description: Rhizoid holdfasts have irregular stellate shapes, with long rope-like roots. Generally four to five primary roots extend from the center of the holdfast. These primary roots (up to 300 μm wide) may split into weakly diverging and tapering, somewhat thinner roots (Plate I, figs 6, 9). Strikingly thinner secondary rootlets (100 to 150 μm wide) extend laterally at high angles from the primary roots (Plate I, figs 10, 11). Even thinner (< 100 μm) rootlets may extend from sides of secondary rootlets or sides of primary roots (Plate I, figs 9, 11). Regardless of their size the roots and rootlets together form a complex plexus (Plate I, 10) wholly attached to a host stem or penetrating into slits between two columnals (Plate I, fig. 13). Roots and rootlets frequently fuse together (Plate I, figs 9, 12) and may run in almost any direction. Growth vector may change abruptly (Plate I, figs

Plate I. Rhizoid holdfasts; Lower Eifelian, Třebotov Limestone; locality Praha-Barrandov, road cut K Barrandovu street; sample Barr: –210. 1 – Two holdfasts in right side (a), top (b) and left side (c) views, PCZCU 2492. 2 – Holdfast in right side (a), top (b) and left side (c) views, showing deformation of host stereome, PCZCU 2514. 3 – Small holdfast in right side (a), top (b) and left side (c) views, PCZCU 2487. 4 – The smallest examined holdfast, PCZCU 2517. 5 – Holdfast in right side (a), top (b) and left side (c) views, with distinct swelling of host stem, PCZCU 2491. 6 – Holdfast in right side (a), top (b) and left side (c) views, with distal roots embedded to host stereome, PCZCU 2493. 7 – Holdfast in top (a) and right side (c) views, PCZCU 2516. 8 – Holdfast in top (a) and side (b) views, with roots around columnal spines, PCZCU 2515. 9 – Holdfast in right side (a), top (b) and left side (c) views showing deformation of a host stereome, PCZCU 2522. 10 – Loose holdfast in top view (a) and its underside (b), PCZCU 2526. 11 – Holdfast in right (a), top (b) and left side (c) views showing non-reaction of a host stereome, PCZCU 2432. 12 – Holdfast in top (a) and left side (b) views, PCZCU 2494. 13 – Holdfast on a columnal (a) with roots attached to an articulum (b), PCZCU 2495. Length of scale bars = 1 mm.

Plate I


1a
1b
1c
2a
2b
2c
3a
3b
3c
4
5a
5b
5c
6a
6b
6c
7a
7b
8a
8b
9a
9b
9c
10a
10b
11a
11b
11c
12a
12b
13a
13b

6, 7, 9), but roots of all sizes are tightly fastened to a host surface. Some rootlets twist round spines of an occupied columnal (Plate I, fig. 8). Parallel growth direction of adjacent rootlets is apparent in some holdfasts (Plate I, fig. 12b). The main growth direction of primary roots attached to a narrow host stem follows elongation of this stem (Plate I, figs 11, 12).

Regardless of their size, all roots and rootlets are primary tubular structures having subcircular to oval cross-sections, with the maximum diameter slightly above the surface of the host stem. A narrow interstice along the root sides (Plate I, figs 11, 12) is developed. A narrow canal goes through the center of each root. Tips of roots and rootlets are narrowly acute and often are more or less submerged into a host stereome (Plate I, figs 5, 7, 9).

The stem base of epibiont is a deep crater-like depression with comparatively thick walls having external diameter between 250 to 800 μm (n = 23; average 525 μm). Surface of articular facet is smooth.

Roots and rootlets of particular holdfast completely or nearly completely surround the stem circumference. Holdfasts generally spread over one (6 holdfasts), two (11 holdfasts), three (3 holdfasts) or even five (one holdfast) columnals. Two attached holdfasts were observed on the same pluricolumnal (Plate I, fig. 1; Plate III, fig. 1). The initial growth point of the holdfast may be on the external face of a columnal (9 holdfasts; Plate I, figs 7–9, 11) but more frequently the larva settled near the suture between columnals (13 holdfasts; Plate I, figs 1–6, 12, 13).

The direction of the stem base of an epibiont is not random. It generally follows an elongation of the host stem but also may diverge at a high angle (Figure 2A). The deviation of the epibiont stem from the surface of host stem may be low, but the majority of epibionts have the stem directed almost perpendicularly to host surface (Figure 2B).

Remarks: Apart of two exceptions (one figured on Plate I, fig. 8), the rhizoid holdfasts were observed exclusively on smooth or weakly spinose

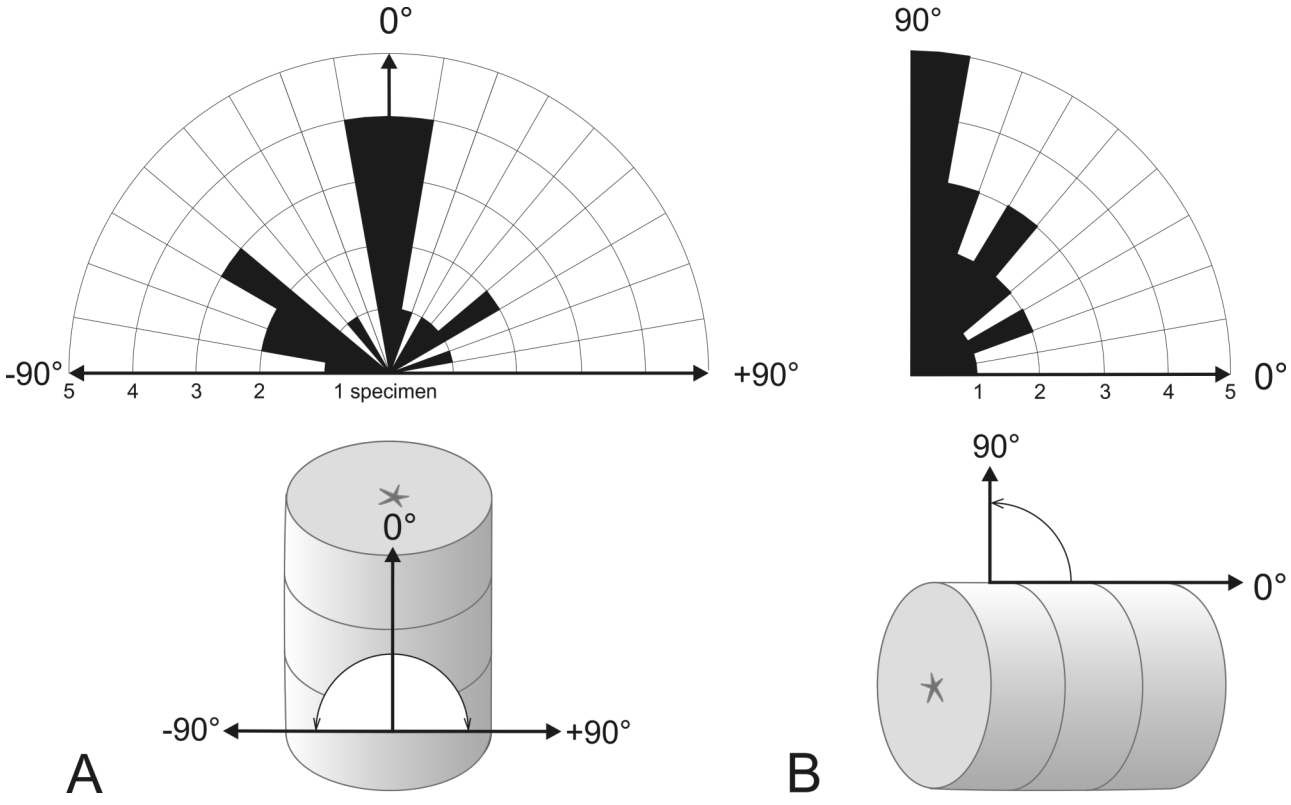


Figure 2. *Rose-diagrams showing the direction of an epibiont stem base in relation to a stem of a given host (A) and a deviation angle of the epibiont stem to the surface of host stem (B). 23 (A) and 20 (B) specimens were examined.*

homoeomorphic stems of circular outline. These columnals may be tentatively referred to *Schyschatocrinus*, *Stenocrinus* and *Salairocrinus*. The diameters of host columnals range from 750 μm to 3 mm, but majority (20 of 23 measured specimens) have a 1.4 to 2.0 mm diameter. The uniform shape of the articulum and the shape of the root plexus suggest that all holdfasts likely belong to one pelmatozoan species. The taxonomic affinity of the epibiont producing rhizoid holdfasts is unclear. The almost uniform size of the stem base, large circular lumen and absence of crenularium suggest small to moderate adult size of the epibiont pelmatozoan. The specimen PCZCU 2517 (Plate I, fig. 4) is distinct by an extremely small size (250 μm) of stem base but this may be related to youth age. At present state of knowledge, any of associated described crinoids cannot be definitely affiliated with the holdfasts.

Stellate and lobate holdfasts

Plate II, figs 1–8, 10–12, 14–16

Material: Seven holdfasts attached to crinoid columnals or pluricolumnals and eight loose holdfasts: figured specimens (PCZCU 2489, PCZCU 2490, PCZCU 2496, PCZCU 2512, PCZCU 2520, PCZCU 2523, PCZCU 2525, PCZCU 2527, PCZCU 2529–PCZCU 2531, PCZCU 2533, PCZCU 2535).

Description: Stellate holdfasts have irregularly stellate to lobate shape, with narrow roots of uneven size. Roots and lobes are tightly fastened to host surface. The roots are gently convex, semicircular to semielliptical in a cross-section. Regardless of their size, the maximum width is at their attached face. Distal parts of roots extend to narrow terminations. Branching of the roots is sparse. The secondary rootlets are markedly smaller that the main roots. Distal parts of roots may complete surround a circumference of a host stem or its substantial part.

Slightly differently shaped roots were observed in two holdfasts. Short lobate extensions (Plate II, fig. 14) or rhizoid-like extensions (Plate I, fig. 16) indicate a different growth of the holdfast stereome.

Stellate rhizoids extend over two (Plate II, figs 1, 2, 4, 5) or more (Plate II, fig. 7) columns of a stem, but other holdfasts were clearly attached to a planar surface (Plate II, figs 10–12, 14, 15). The origin of the planar substrate is ambiguous, but the grooved underside of one holdfast (Plate II, fig. 16) resembles an external costellation of a strophomenide brachiopod. Only one holdfast (Plate II, fig. 7) grew over a heteromorphic stem, others (Plate II, figs 1–6) fastened to homeomorphic circular stems.

Some holdfasts have larger and a weakly elevated articular facet with a featureless central lumen surrounded by a narrow crenularium (Plate II, figs 1b, 4b, 6b, 9, 14a). In other holdfasts, the articular facet with only a few high triangular crenellae surround a funnel-shaped depression (Plate II, figs 2a, 3a, 5b, 8a). A few holdfasts display flat articular facets with fine crenellae and a minute lumen (Plate II, fig. 11, 16a). Based on the facing of the articular faces it is suggested that the stem of epibiont rested almost perpendicular to the host stem.

Remarks: Different crenulation and shape of articular facets of holdfasts suggest that the holdfast belong to few different crinoid taxa. Apart of undetermined stems, these holdfasts were observed on columnals of *Schyschatocrinus* and *Stenocrinus*. Unlike the rhizoid holdfasts the stellate holdfasts likely belong to more crinoid taxa. Similar stellate holdfasts fixed to heteromorhic pluricolumnals were described by Gluchowski (2005; fig. 5F, G) from the upper Eifelian of the Holy Cross Mountains in Poland.

Broadly lobate holdfasts

Plate II, figs 9, 13; Plate III, figs 6, 8, 11

Material: Eight loose holdfasts: figured specimens (PCZCU 2513, PCZCU 2521, PCZCU 2524, PCZCU 2534) and four unfigured specimens.

Description: Lobate holdfasts have a highly irregular lobate shape with gently elevated stem base. Their size is 6 mm or more. Their upper surface is uneven, smooth to irregularly wrinkled. The holdfast periphery often overgrew the edge of the substrate (Plate II, fig. 13; Plate III, fig. 8) or enveloped a nearby bioclast (Plate II, fig. 9). Some stem bases form a shallow depression surrounded by a narrow articulum (Plate III, figs 6, 11) but other holdfasts possess a coarse crenularium and pentastellate lumen (Plate III, fig. 8). Margins of holdfast extend into small short lobes (Plate III, fig. 6), broad and robust lobes (Plate III, fig. 8) or rhizoid or digitate extensions (Plate III, fig. 11). The underside of holdfasts imprinted a subplanar

Plate II


1a
1b
1c
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3b
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4c
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5c
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6c
7a
7b
8a
8b
9
10a
10b
11
12
13a
13b
14a
14b
15a
15b
16a
16b

featureless substrate, the costellation of a brachiopod shell (Plate III, fig. 8b) or a cylindric substrate, likely a crinoid stem or a small cephalopod shell (Plate III, fig. 6). A bioclaustration of a foraminifer test attached to planar surface was observed (Plate II, fig. 13b). Two mutually overgrowing holdfasts were observed (Plate III, fig. 11).

Remarks: Lobate holdfasts are markedly larger than the rhizoid and stellate holdfasts. Their host object is generally unpreserved. The rarity of larger holdfasts and absence of matching substrate among the studied material have many causes. One reason is the rarity of larger crinoids in original life association which is apparent from the size frequency of columnals in the samples. Also important is the higher brittleness of loose holdfasts compared with holdfasts fixed to pluricolumnals. Loose larger sheet-like holdfasts detached from a host surface were more easily disintegrated into small pieces and were efficiently affected by weathering processes more than smaller holdfasts fastened to more resistant crinoid ossicles.

Cirral holdfasts

Plate III, figs 4–7, 10

Material: Ten holdfasts attached to crinoid columnals or pluricolumnals: figured specimens (PCZCU 2521, PCZCU 2537–PCZCU 2540) and five unfigured specimens.

Remarks: Small stereomic sheets of subcircular, discoid and unevenly lobate outlines likely represent attachments of cirral outgrowths of crinoids. These irregular sheets extend laterally or terminally from thin cylindrical ossicles showing a distinct lumen. Some of these cylindrical ossicles show sutures (Plate III, fig. 5). Cirrals are attached perpendicularly (Plate III, fig. 7) or tangentially (Plate III, fig. 4) to a host surface. Adhesive sheets are fixed to upper surface of the holdfast of another indeterminate crinoid (Plate III, fig. 11) or the sheet expands by few lobes over the surface of a pluricolumnal of *Simakocrinus diligens* Prokop, 2013 (Plate III, fig. 10).

Epibiont foraminifers

Plate IV

Material: Fourteen specimens cemented to bioclasts (PCZCU 25498–PCZCU 2511).

Description: Two taxa of cemented epibiont foraminifers were determined. Tests of *Tolypammina* are hemitubular with a distinct ovoid proluculus followed by a chain of two to five weakly defined chambers subsequently extended into a long entire weakly and irregularly bent test. Its proluculus is cca 170 μm wide. The total length of a tube may reach 2.4 mm having the maximum width of 200 μm near the aperture.

Psammosphaera form a semiglobular subcircular to semielliptical test attached by its flat lower side to a hard surface. Test are 570 to 800 μm long, 500 to 600 μm broad, and up to 600 μm high. The circular aperture is only 25 μm large.

Remarks: Holcová (2002) summarized data about foraminifers from the Silurian and the Devonian of the Prague Basin. Our cemented foraminifers can be attributed to *Tolypammina bulbosa* (Gutschick & Treckman, 1959) and *Psammosphaera cava* Moreman, 1930. The cemented test of these foraminifers are uncommon on the surface

Plate II. Stellate and lobate holdfasts; Lower Eifelian, Třebotov Limestone; locality Praha-Barrandov, road cut K Barrandovu street; sample Barr: –210. 1 – Stellate holdfast in right side (a), top (b), left side (c) and back (d) views showing weak engulfing by the host stereome, PCZCU 2488. 2 – Stellate holdfast in top (a) and left side (b) views, showing crenella on articulum, PCZCU 22523. 3 – Small holdfast in top (a) and left side (b) views, PCZCU 2520. 4 – Stellate holdfast in right side (a), top (b), and left side (c) views showing thin distal roots, PCZCU 2490. 5 – Stellate holdfast in right side (a), top (b), and left side (c) views showing branching of distal roots and crenella at articulum, PCZCU 2489. 6 – Small stellate holdfast in right side (a), top (b) and left side (c) views showing weak overgrown by a host stereome, PCZCU 2496. 7 – Holdfast in top (a) and left side (b) views fixed to heteromorphic stem, PCZCU 2512. 8 – Loose stellate holdfast (a) and its underside (b), PCZCU 2536. 9 – Lobate holdfast overgrowing a loose columnal, PCZCU 2528. 10 – Loose small stellate holdfast (a) and its planar underside (b), PCZCU 2527. 11 – Loose small stellate holdfast from a planar surface, PCZCU 2525. 12 – Loose small stellate holdfast from a planar surface, PCZCU 2529. 13 – Large lobate holdfast (a) and its underside (b) with folded lobes and a bioclaustration of a semiglobular foraminifer *Psammosphaera* sp. attached on surface of unpreserved planar substrate (b), PCZCU 2533. 14 – Loose small lobate holdfast (a) and its planar underside (b), PCZCU 2530. 15 – Loose small lobate holdfast (a) and its wrinkled underside (b), PCZCU 2531. 16 – Loose small rhizoid holdfast (a) and its grooved underside with likely imprinted costellation of a subplanar brachiopod shell (b), PCZCU 2535. Length of scale bars = 1 mm.



Plate III. Diverse holdfasts and a malformed columnal; Lower Eifelian, Třebotov Limestone; locality Praha-Barrandov, road cut K Barrandovu street; sample Barr: –210. 1 – Mutually overgrowing rhizoid holdfasts in top (a) and left side (b) views without any stereomic response of a host stem, PCZCU 2518. 2 – Rhizoid holdfasts deeply overgrown by stereome of a host stem, PCZCU 2519. 3 – Two rhizoid holdfasts almost entirely overgrown by strongly swollen stereome of a host stem, PCZCU 2497. 4 – Cirral holdfast on a host stem, PCZCU 2537. 5 – Cirral holdfast showing sutures on a host stem, PCZCU 2539. 6 – Small cirral holdfast attached to surface of large lobate holdfast, PCZCU 2521. 7 – Small cirral holdfast attached subperpendicularly to large columnal, PCZCU 2538. 8 – Loose large lobate holdfast with distinct articulum, pentastellate lumen and wrinkled lobes (a), and its underside with lobes folded over a subplanar grooved substrate, likely a brachiopod shell (b), PCZCU 2513. 9 – Malformed crinoid columnal, PCZCU 2534. 10 – Lobate (?)cirral holdfast on a stem of *Simakocrinus diligens* Prokop, 2013, PCZCU 2540. 11 – Loose large lobate holdfasts with attached another smaller holdfast (a), and its uneven underside with rhizoid extensions, PCZCU 2524. Length of scale bars = 1 mm.

of bioclasts. Fourteen cemented tests were observed among 6500 examined crinoid columnals. Only six specimens of *Psammosphaera* sp. and eight tests of *Tolypammina* sp. have been observed on the surface of bioclasts. In contrast, loose tests are fairly common among loose fossils of the white beds. Examined tests of *Psammosphaera* sp. are fixed to the exposed surface of columnals (Plate IV, figs 12–14) but were observed directly on an articulum and inside a food groove of the pinnular plate.

Tolypammina sp. cemented on diverse substrates. These are brachiopod shells (Plate IV, figs 1, 2, 5), crinoid columnals (Plate IV, fig. 6), inner side of calceocrinid cups (Plate IV, figs 3, 4), cup plates of other crinoids (Plate IV, fig. 8), and the inner side of cystoid plates (Plate IV, fig. 7). All *Tolypammina* tests except one (Plate IV, fig. 6) preferably grew on concave surfaces of the substrate. Growth of foraminifer tests on inner surfaces of brachiopod shells, on an articulum and over a suture between columnals, and the inner sides of cups of crinoids and cystoids was possible after release of plates and shells of hosts and their subsequent exposure on the sea floor for a certain time. This conclusively document an occupation of bioclasts by dead organisms.

Holcová (2002) summarized data about foraminifers from the Silurian and the Devonian of the Prague Basin. Our cemented foraminifers can be attributed to *Tolypammina bulbosa* (Gutschick & Treckman, 1959) and *Psammosphaera cava* Moreman, 1930.

Stereomic malformation

Plate III, fig. 9

Material: One columnal (PCZCU 2534).

Description: One long columnal demonstrates a strong malformation. The one articular facet (lower) has a regular shape with lumen, a narrow crenularium and large areola. The opposite (upper) articular facet has only two-thirds diameter and is surrounded by seven deep pits in a stereomic swelling. The pits are uniform in size and of uneven outline and all except for one (Plate III, fig. 9a) closely border the articular facet.

Remarks: Pits inside a stereomic swelling in crinoid columns have been described by more authors (Franzén 1974, Brett 1978, Meyer & Ausich 1983, Vinn *et al.* 2015), some being interpreted as a swelling after infestation by byronids (Welch 1976, Werle *et al.* 1984). Smaller size of upper articulation facet is likely the result of an infestation by parasites. The regular stereomic growth of a given host was hampered by seven parasites; the columnal became hypertrophied and adjoining columnal did not attain the regular size.

DISCUSSION

Many kind of organism are preserved encrusting crinoid pluricolumnals. Following the synopsis of Meyer & Ausich (1983), in order to evaluate such associations, this question must be addressed: Was the attached organism an epizoan living on a live crinoid or the crinoid ossicle was only a sedimentary grain at the time of attachment?

In the case of foraminifers, there is no doubt that they cemented to substrates forming coarse sedimentary calcitic grains. Interior of brachiopods, lumens and other similar surfaces of crinoids might be utilized after the death of live specimens and the clearing away of the soft tissues covering their surfaces. Scavengers and microbial decomposition of tissues cleaned the substrate rapidly. One can speculate on material from sample Barr: –210 that *Tolypammina* sp. preferred a protected or cryptic habitat, because its tests dominantly occupied the concave surfaces. One test of *Psammosphaera* sp. was also observed on a protected site inside a food groove of a crinoid ossicle, but others grew on much more exposed surfaces. However, the examined cemented tests represent only a minority of foraminifers on the sea bed. The majority of loose tests among washed fossils give evidence they were attached to any substrate as evidenced by their flat undersides, but the substrate is not preserved. Unlike *Tolypammina* and *Psammosphaera* tests which have been observed both cemented and loose, associated test of *Ammodiscus* are represented only by loose specimens. Holcová (2003) assessed the mode of life and life associations of foraminifers from the Třebotov Limestones. She suggested a higher tolerance of *Tolypammina* to high-energy environment and a negative correlation between *Tolypammina* and *Ammodiscus* occurrences in the Třebotov Limestone sections. Similar saccamminid foraminifers on pluricolumnals suggesting their epibiont mode of life have been mentioned by Głuchowski (2005) from the Eifelian of Poland.



Plate IV. Epibiont foraminifers; Lower Eifelian, Třebotov Limestone; locality Praha-Barrandov, road cut K Barrandovu street; sample Barr: –210. 1, 2, 5 – *Tolypammina* sp., tests cemented on concave inner surfaces of brachiopods, PCZCU 2499, PCZCU 2505, PCZCU 2500. 3, 4 – *Tolypammina* sp., tests cemented inside cups of calceocrinid, PCZCU 2503, PCZCU 2498. 6 – *Tolypammina* sp., test cemented to articulum of a columnal, PCZCU 2510. 7 – *Tolypammina* sp., test cemented to plate of a pleurocystoid, PCZCU 2502. 8 – *Tolypammina* sp., test cemented to inner side of a crinoid crown plate, PCZCU 2501. 9 – *Tolypammina* sp., test cemented over a suture of a crinoid stem, PCZCU 2504. 10 – *Psammosphaera* sp., test cemented in food groove of a crinoid brachial plate, PCZCU 2506. 11 – *Psammosphaera* sp., test cemented on an articulum of crinoid brachial plate, in top (a) and side (b) views, PCZCU 2509. 12–14 – *Psammosphaera* sp., tests cemented to surface of crinoid columns in top (a) and side (b) views, PCZCU 2511, PCZCU 2507, PCZCU 2508. Length of scale bars = 1 mm.

Almost all rhizoid-type holdfasts attached to pluricolumnals conclusively grew on living crinoids. This is evident from stereomic swelling of the host. Our material provides a whole range of stereomic responses, from a weak overgrowth of distal rootlets to complete engulfing of the holdfast by a host stereome. The early stage of epibiont (Plate I, figs 11, 12; Plate III, fig. 1) shows almost no stereomic reaction. The stereome reaction begin with engulfing of distal parts of epibiont rootlets, which came about due to being partly to almost entirely submerged below the epiface of host columnals (Plate I, fig. 6, 9). The continous expansion of the host stereome engulfed the holdfast and left it free only on the central part of the holdfast (Plate III, fig. 2). Finally, the holdfast is completely engulfed by a stereome and the articulum of epibiont is covered by the stereome of the host (Plate III, fig. 3). The host stalk became conspicuously thicker, with an uneven epiface, and its sutural furrows almost disappear. The swelling of a host stereome is stronger near distal rootlets than around the proximal roots and below the central area with stalk base of the epibiont. The stereomic response of host was likely suppressed around the settled larva. However, during the subsequent expansion of the holdfast the epibiont's ability to reduce the reaction of host stereome decreased.

The similar behavior of stereomic overgrowths is apparent in stellate holdfast attached to a crinoid stalk. Distal rootles of attached crinoid are distinctly overgrown by a host stereome (Plate II, figs 1a, c, d; 5a, c; 6c) but stereome reaction is weak near the center of holdfasts (Plate II, figs 5b, 6b). However, some stellate holdfasts induced none stereomic reaction. Whether the stereomic reaction was weak or whether the epibiont grew on a stalk of dead host is unclear. No stereomic swellings of a given host was observed on cirral holdfasts.

The initial site from which a holdfast expanded is often located (about 50 % of examined holdfasts) just near suture furrows of a given host stalk. This preference may be related with a suggested protective nature on a surface near suture furrow and corresponding selective settlement of the epibiont larva. The narrow band around the suture furrow may represent a safer site for settlement of the larva due a weaker stereomic response than the epiface of a host column.

CONCLUSION

Diminutive crinoid holdfasts, which belong to many species, and cemented tests of foraminifers *Psammosphaera* and *Tolypammina* were observed on coarse bioclasts in weathered limestones of the Daleje-Třebotov Formation in Praha-Barrandov.

Epibiont crinoids attached to stalks of other host crinoids often induced swellings of host stalk stereome. The extended stereome was able to overgrow the distal roots of holdfasts, later also the proximal roots, and after some time could overgrow over the entire holdfast. The epibiont crinoid was able, at least for a limited time, to control its own growth direction relative to the direction of a host stem. The data conclusively document that epibiont crinoid larva settled onto a stalk of a living crinoid and initial growth of the epibiont took place on a living host. However, some other observed crinoid holdfasts were attached to larger, likely loose bioclasts from disintegrated crinoids and other invertebrates.

Unlike the crinoids, the cementing foraminifers grew on loose bioclasts on a sea bed. This is evidenced by locations of tests on articular facets, interiors of valves and crevices. Some individuals preferred sheltered concave, likely representing cryptic surfaces.

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